ZOOLOGIA 35: e12487
ISSN 1984-4689 (online)
zoologia.pensoft.net

RESEARCH ARTICLE

Ecology of the snake *Atractus paraguayensis* (Dipsadidae) in southern Brazil

Noeli Zanella[1], Fernanda D'Agostini[2]

[1]*Instituto de Ciência Biológicas, Universidade de Passo Fundo. Rodovia BR 285, São José, 99052-900 Passo Fundo, RS, Brazil.*
[2]*Universidade do Oeste de Santa Catarina. Rua Getúlio Vargas 2125, Flor da Serra, 89600-000 Joaçaba, SC, Brazil.*
Corresponding author: Fernanda D'Agostini (fernanda.dagostini@unoesc.edu.br)

http://zoobank.org/993A04D5-5899-44F5-AADA-904B08E9013B

ABSTRACT. Knowledge of snake ecology is important to support conservation strategies. *Atractus paraguayensis* Werner, 1924 is a dipsadidae with semi fossorial habits distributed throughout southern Brazil. We analyzed the morphology, seasonality and reproductive biology of this species in a subtropical area in southern Brazil by combining material from scientific collections and field data. We found that females have a larger body size than males and that the reproductive cycle of females is seasonal, with vitellogenesis occurring in the warmer months of the year. Males exhibited no differences in testicle volume throughout the year; however, mating likely occurs in the spring when males are more active. Recruitment of newborns occurs in late summer. The number of individuals collected during the hottest months (September through February) was significantly higher than the number of individuals collected during the colder months. Our results, which reveal sexual dimorphism in the species and seasonal breeding restricted to warm months, contribute important information about this species' biology.

KEY WORDS. Activity patterns, reproduction, seasonality, subtropical region.

INTRODUCTION

Snake biology is commonly discussed in the literature, and reproduction of neotropical snakes is a recurrent topic (Bizerra et al. 2005, Prudente et al. 2007, Gomes and Marques 2012, Bellini et al. 2013, Panzera and Maneyro 2013, Marques et al. 2014). The popularity of this topic is likely due to the importance of these studies to the general field of ecology. Modes and cycles, fecundity, and sexual dimorphism (SSD) are among the most studied reproductive traits (Pizzatto et al. 2008, Prieto et al. 2012, Braz et al. 2014). These studies contribute to our understanding of the general reproduction patterns of neotropical snakes. Snakes may present SSD (e.g. in body size; females larger than males), tail size (males' tails longer than females' tails), the quantity or shape of scales, and sexual dichromatism (Shine 1994, Pizzato et al. 2007). Beyond morphological differences, these snakes may have well-defined reproductive traits, such as females with double vitellogenesis, where the primary has transparent or whitish-colored follicles (sexually immature and mature females), and the secondary has yellow coloring at the yolk (sexually mature females) (Shine 1994, Almeida-Santos and Salomão 2002). Males have deferent ducts, which can be smooth (sexually immature males) or convoluted (sexually mature males) (Shine 1994, Pizzato et al. 2007). The reproductive period may vary throughout the year, and environmental factors such as temperature, humidity and photoperiod may influence snake reproduction. A greater predominance of females with secondary vitellogenesis generally occurs during these seasonal cycles because the increase in temperature influences their metabolic rate (Vinegar 1974). *Atractus* Wagler, 1828 is widely distributed in the neotropical region and can be found from Panama to Argentina (Giraudo and Scrocchi 2000). This genus includes small to moderate sized serpents with secretive habits (semifosssorial or cryptozoic) that feed on worms, arthropods and mollusks (Martins and Oliveira 1999, Balestrin et al. 2007). *Atractus paraguayensis* Werner, 1924, which can be found in southern Brazil, Argentina and Paraguay (Passos et al. 2010), displays terrestrial or fossorial habits. However, there is limited information about the natural history of this species.

Here, we present data pertaining to the reproductive biology and activity patterns of *A. paraguayensis* in southern Brazil. We base our analysis on specimens preserved in herpetological collections and specimens collected in pitfall traps.

MATERIAL AND METHODS

We examined 163 specimens of *A. paraguayensis* from southern Brazil, 126 of which were preserved specimens from the following collections: Fundação Zoobotânica (FZB), Universidade Federal do Rio Grande do Sul (UFRGS), Universidade de Passo Fundo (UPF), Universidade do Oeste de Santa Catarina (UNOESC) and Universidade de Chapecó (UNOCHAPECO). The remaining 37 specimens were collected using pitfall traps.

We obtained the following measurements for each examined specimen: (1) snout-vent length (SVL); (2) tail length (TL); (3) sex; (4) juvenile or adult (males were considered to be adults if enlarged testes and opaque deferent ducts were observed (Shine 1982), and females were considered to be adults if either ovarian follicles in vitellogenesis or oviductal eggs were observed (Shine 1980); (5) for female specimens, diameter of the largest ovarian follicles, diameter of the largest egg, number of ovarian follicles in vitellogenesis (>10 mm), and number of oviductal eggs. According to Shine (1994), the degree of sexual size dimorphism (SSD) was calculated as follows: mean SVL of the larger sex divided by the (mean SVL of the smaller sex) – 1. This index is positive if females are the larger sex and negative if males are larger.

In our analysis of SSD, we included only adult individuals. We counted oviductal eggs and neonates to estimate fecundity. Reproductive frequency was estimated by the percentage of females apt for reproducing (with ovarian follicles or oviductal eggs) found in the sample (Pizzatto 2005). We used linear regression to test the relation between female body size (SVL) and fecundity. We used a t-test to analyze morphological differences between males and females and to compare variations in testicular volume between seasons to determine reproductive activity in males. We used a chi-square test to analyze seasonality. For all of our analyses, differences were considered significant at $\alpha = 0.05$.

The field activities occurred at Parque Natural Municipal de Sertão (PNMS) (28°02'31"S, 52°13'28"W), which is located in the municipality of Sertão, northern Rio Grande do Sul. This area is composed of remnant Atlantic Rain Forest and transitional forests and ranges from the pine forests of Campos de Cima da Serra to the forests of the Uruguay River basin. The mixed forest vegetation in this region is known as Mixed Ombrophilous Forest (Quadros and Pillar 2002). The region has an altitude gradient ranging from 630 to 740 m and a subtropical humid climate. The average temperature of the hottest month exceeds 22 °C, and the minimum average temperature is 13.2 °C. Rainfall is well distributed, with an average of 1,787 mm per year (Embrapa 2011).

We used the adult and juveniles specimens collected from the pitfall traps to analyze seasonal patterns. We recorded the following morphometric measures for the collected specimens: (1) SVL and (2) TL. We also verified the body mass of individuals using a dynamometer with a scale with a precision of 0.1 g. Finally, we verified the animals' sex.

Pitfalls with drift-fences (Corn 1994) were installed at four different plots in the study area. Each plot was composed of eight containers with a capacity of 150 l, for a total of 32 buried containers. Each container was 1 m high. The containers were arranged in a straight line in the forest, 10 m apart from one other. They remained open from May 2008 through April 2010 and were inspected 2–3 times per week. Subjects were marked, and no recaptures occurred during this period. There are accordingly no overlapping data. We determined the pattern of annual activity using the number of snakes collected in the pitfalls. Additionally, we included specimens deposited in collections collected between 1975 and 2013.

RESULTS

Body size, sexual dimorphism and sexual maturity

Juvenile SVL averaged 176.05mm (range = 111-297 mm, standard deviation (SD) = 55.04 mm, n = 17) and TL averaged 20.04 mm (range = 14.28–42.43 mm; SD = 8.57 mm). Mature females had an average SVL of 368.92 mm (range = 277-462 mm; SD = 42.11 mm, n = 31), and mature males had an average SVL of 324.46 mm (range = 213-442 mm; SD = 49, n = 43). The difference in SVL between males and females was statistically significant ($t = 3.49$, $p = 0.0005$). The TL of adult males and females was similar ($p = 0.1185$). Females reach sexual maturity (SVL = 277 mm) with a larger body size than males (SVL = 213 mm). The degree of SSD was 0.18.

Reproductive cycle, fecundity and reproductive frequency

Females exhibited vitellogenic follicles (> 10 mm) from November through January and eggs in their oviducts in November and December, the hottest months of the year (Fig. 1). This finding indicates a seasonal reproductive cycle. The relation between clutch size and female SVL was weak and not statistically significant ($r^2 = 0.0418$, $p = 0.6608$, n = 24). We observed 3–13 vitellogenic follicles ($\bar{x} = 8$, SD = 2.2, n = 21) and 3–8 eggs in the oviduct ($\bar{x} = 5.7$, SD = 2.5, n = 3), indicating that clutch size is independent of female size (Fig. 2).

Males did not exhibit a statistically significant difference in testicular volume during warm (September through March) and cold (April through August) months ($t = 1.012$, $p = 0.4816$, $n = 15$) (Fig. 3). Mating likely occurs in the spring when males are more active.

Activity patterns

We determined the annual activity pattern of *A. paraguayenis* using a sample of 130 individuals (93 from collections and 37 captured in the pitfalls). The number of individuals collected during the hottest months was significantly larger than the number of individuals collected during the coldest months (chi-square = 16.4, $p = 0.0116$). The data indicate that females were more active from August through December and that males were more active from September through April (Fig. 4).

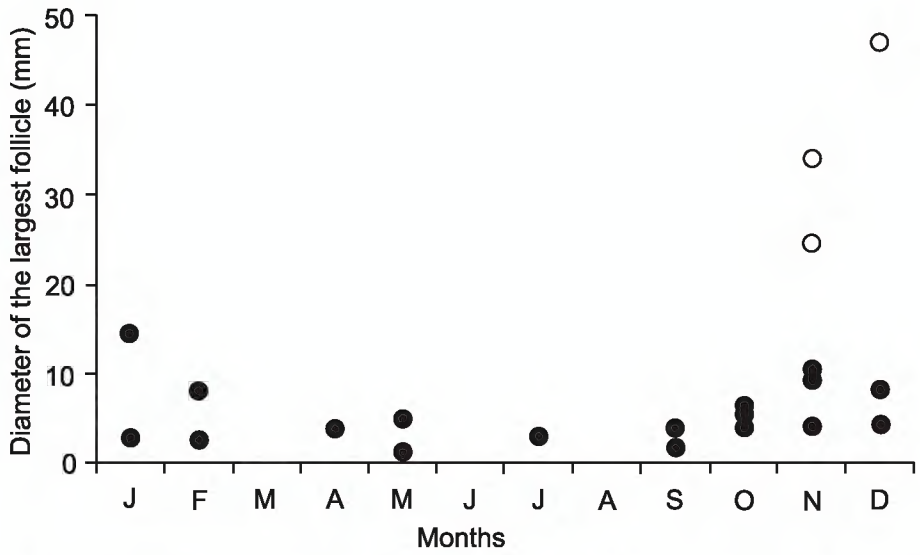

Figure 1. Seasonal variation in diameter of the largest ovarian follicle or eggs in females of *Atractus paraguayensis* from southern Brazil. Solid circles = ovarian follicles; open circles = eggs.

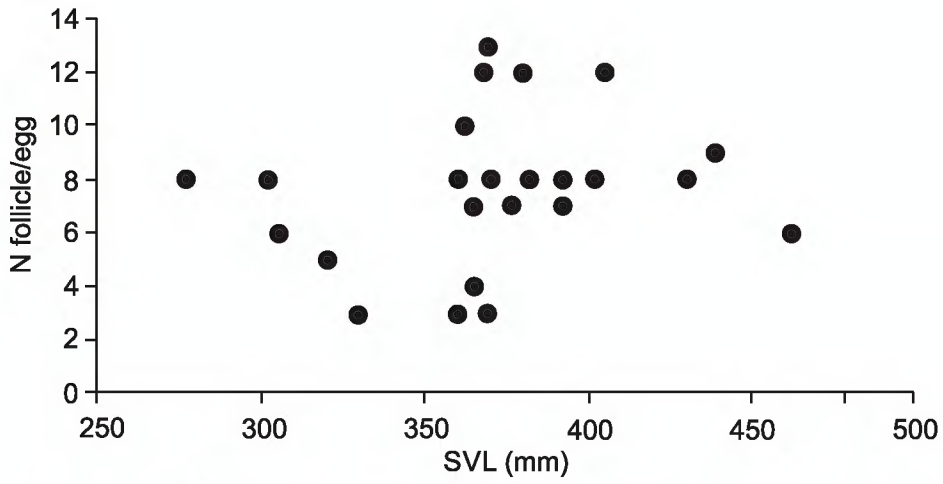

Figure 2. Relation between SVL from females and fecundity (number of follicles or eggs in the oviducts) in *Atractus paraguayensis*, southern Brazil.

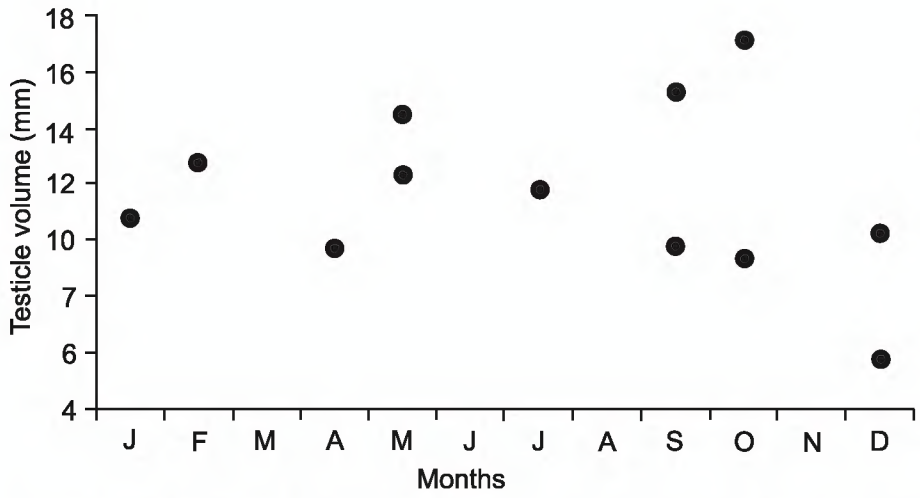

Figure 3. Seasonal variation of testicular volume in *Atractus paraguayensis* from southern Brazil.

Females exhibited a peak in November when we recorded 34.4% of all individuals; males exhibited a peak in September when we recorded 31.6% of all individuals.

We found *A. paraguayensis* activity in the forest, but the records that we analyzed from the collections also indicated that these snakes inhabit open, anthropic areas.

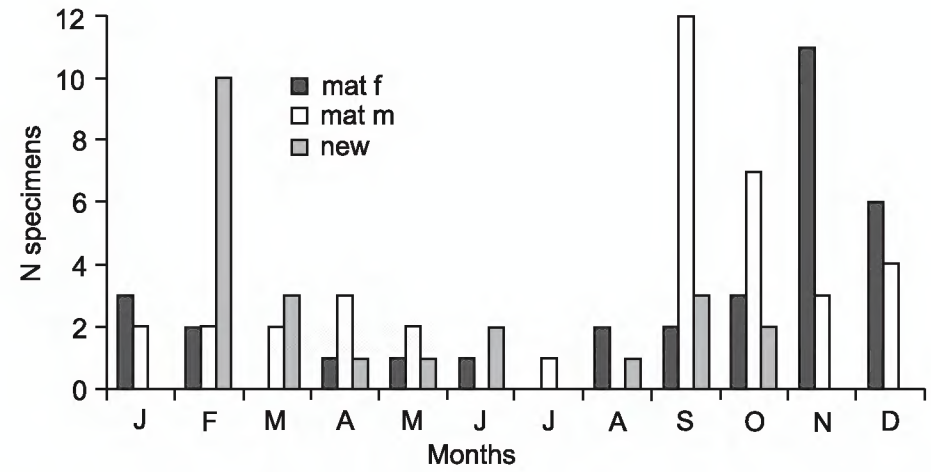

Figure 4. Abundance of *Atractus paraguayensis* using individuals from collections and pitfalls, from May 2008 to April 2010, at Parque Natural Municipal de Sertão. Mat f = Mature females; mat m = mature males.

Juvenile specimens were collected mainly from February through October (n = 23) (Fig. 4). Seven eggs were laid in captivity on January 12, 2008, six of which hatched on February 26, 2009. The average SVL was 113 mm (range = 100–120 mm).

DISCUSSION

Male and female *A. paraguayensis* have different body sizes when they attain sexual maturity. This trend has been noted for the majority of snakes (Gomes and Marques 2012, Alencar and Nascimento 2014, Marques et al. 2014, Resende and Nascimento 2015). However, females tend to be larger than males. The larger body size for females is common in snakes, and females tend to be the larger sex in species in which male-male combat has not been recorded (Shine 1994). The larger size of the female body offers advantages such as greater fertility, which results in larger litters, and ultimately ensures greater reproductive fitness (Ford and Seigel 1989, Rivas and Burghardt 2001), although this trend was not recorded in this study.

In terms of specimen size and sexual maturity, we observed that females attained sexual maturity when they were larger than males. The available evidence suggests that the age that females attain sexual maturity might be delayed compared with that of males of the same species due to high energy-reproduction costs (Shine 1978, 1994). Later maturity in females may represent a tradeoff in which sexual maturity is delayed so that larger clutches of larger eggs can be laid (Pinto and Fernandes 2004). However, larger females have been believed to be favored by natural selection because they can produce larger eggs and clutches (Ford and Seigel 1989). Clutch size is typically correlated with the female body size (Shine 1994), but we did not find any correlation between SVL and fecundity. The r of *A. paraguayensis* cannot be considered to be low (3–13 follicles or eggs) because other characteristics – such as the size of eggs and hatchlings and the relative weight of the clutch – can be included to estimate fecundity (Seigel and Ford 1987). Larger species, such as *A. major*

Boulenger, 1894 (723 mm) and *A. torquatus* (Duméril, Bibron & Duméril, 1854) (754 mm) produce similar postures (Martins and Oliveira 1993, 1999) (6–12 and 7–8 eggs, respectively). Smaller species, such as *A. pantostictus* Fernandes & Puorto, 1993 (248 mm) (Resende and Nascimento 2015) and *A. reticulatus* (Boulenger, 1885) (335 mm) (Balestrin and Di-Bernardo 2005), exhibit small clutches (2–4 and 1–3 eggs, respectively). Larger females may produce larger or more offspring, or have higher reproduction frequencies (Shine 1988). However, demonstrating that clutch size increases with maternal size is not sufficient to infer that natural selection should favor large female body size (Shine 1988). The lack of correlation between SVL and fecundity was also recorded for *Thamnodynastes hypoconia* (Cope, 1860) (Bellini et al. 2013): larger females producing fewer eggs were noted. These authors suggest that the lack of correlation may be related to phylogenetic conservatism regarding the number of embryos rather than an advantage in fecundity associated with female size. Although other *Atractus* species exhibit a relation between fecundity and body size, the absence of this correlation in *A. paraguayensis* may be influenced by other factors (e.g. habitat use, feeding habits, phylogeny).

In *A. paraguayensis*, SSD was moderate and male-male combat is not expected from members of the family Dipsadidae (Bizerra et al. 2005), confirming a pattern of dimorphism of the species. Shine (1994) found that snakes that do not behave this way have larger SSD and more sexual selection, but this relation is strongly influenced by phylogeny.

The reproductive cycle of females of *A. paraguayensis* is seasonal: vitellogenic follicles and eggs occur from November through January, which is spring and summer in southern Brazil, the warmest periods of the year. These results indicate that moisture and temperature might be factors influencing the reproductive seasonality of the species. This seasonal cycle has been record for other snakes in subtropical areas: It was recorded for *A. pantostictus* in southeastern Brazil, with mating, secondary vitellogenesis, pregnancy, oviposition and recruitment occurring during the rainy season (Resende and Nascimento 2015); and for *A. reticulatus* in southern Brazil, which has a restricted reproductive cycle from November through January (Balestrin and Di-Bernardo 2005), corroborating the data recorded in this study. We also found a predominance of males in the spring, which indicates the males' reproductive seasonality. However, we did not note seasonal differences in testicular volume, which could indicate a lack of seasonal cycle (see discussion below). Seasonal activity among snakes can be influenced by many factors such as temperature, humidity, rainfall and food availability (Lillywhite 1987, Gibbons and Semlitsch 1987); low temperatures can significantly reduce snake metabolic rates and consequently reduce activity (Lillywhite 1987). In the Brazilian temperate region, temperature is one of the primary factors responsible for the low activity of snakes, and it affects reproductive patterns (Di-Bernardo et al. 2007, Panzera and Maneyro 2013). Another noteworthy fact is that oviparous species need to lay their eggs during the warm period of the year because the warm weather benefits egg incubation (Vinegar 1974), thereby contributing to reproductive seasonality.

As noted previously, a pattern that influences the activity of snakes is their reproductive cycle (Gibbons and Semlitscht 1987). Marques et al. (2000) found that reproduction conditions might determine an increase in locomotor activity influenced by abiotic factors (rainfall). Tropical and subtropical snakes exhibit relatively high variability in the length of their reproductive cycles, a pattern that is usually seen as a result of seasonal variation in climate, availability of prey or both (Vitt 1987, Mathies 2011). The months in which we noted the largest number of individuals correspond to the months with the highest temperatures. This species has fossorial habits, and the small number of individuals caught in the winter period might be explained by low temperatures that resulted in decreased metabolism and consequently limited their activity. Females are more active during vitellogenesis, which occurs during the warmest period, when they could be looking for appropriate locations for thermoregulation (Pizzatto et al. 2007, Gomes and Marques 2012). The duration of the reproductive cycle of *A. paraguayensis* appears to be phylogenetically conservative like other species whose continued reproductive cycles have not been recorded (Bizerra et al. 2005, Pizzatto et al. 2008). Males, on the other hand, become more active during the mating season, probably when they are looking for females (Gibbons and Semlitsch 1987, Gomes and Marques 2012).

The volume of the testis of snakes may reflect spermatogenic activity (Almeida-Santos et al. 2006). *A. paraguayensis* presents no seasonal differences in testicular volume between warm and cold seasons, a pattern that is rarely recorded in snakes (Seigel and Ford 1987). This finding might indicate that males are reproductively active throughout the year. To confirm this pattern, analysis histological to correctly describe male reproductive cycles would be necessary (Mathies 2011, Rojas et al. 2013). There are many species wherein one or both sexes exhibit dissociation of gonadal activity and mating (Crews 1984). Dissociation of vitellogenesis has been observed for *Dipsas neivai* Amaral, 1923 females, although males have demonstrated an association between sexual intercourse and spermatogenesis (Alves et al. 2005).

This study provides an overview of the ecology of *A. paraguayensis*. Their characteristics – reproductive age, SSD and seasonality – appear to be common to many South American Dipsadidae. Therefore, this information contributes to elucidating the reproductive and activity patterns of this species.

ACKNOWLEDGMENTS

The authors would like to thank the curators of the scientific collections and the academic course of Biological Sciences of the UPF for help with the field activities. NZ would also like to thank CNPq for their assistance with part of the activities

(Proc. 475796/2007-1) and the licenses granted by Ibama/Sisbio (14543-1/2009 and 26826-1/2011). This manuscript was translated by American Manuscript Editors.

LITERATURE CITED

Alencar LRV, Nascimento LB (2014) Natural history data of a common snake suggest inter-populational variation and conservatism in life history traits: the case of *Erythrolamprus poecilogyrus*. Herpetological Journal 24: 79–85.

Almeida-Santos SM, Salomão MG (2002) Reproduction in neotropical pitvipers, with emphasis on species of the genus *Bothrops*. In: Höggren M, Schuett GW, Greene H, Douglas ME (Eds) Biology of the vipers. Eagle Mountain Publishing, Carmel, 445–462.

Almeida-Santos SM, Pizzatto L, Marques OAV (2006) Intra-sex synchrony and inter-sex coordination in the reproductive timing of the Atlantic coral snake *Micrurus corallinus* (Elapidae) in Brazil. Herpetological Journal 16: 371–376.

Alves FQ, Argolo AJS, Jim, J (2005) Biologia reprodutiva de *Dipsas neivai* Amaral e *D. catesbyi* (Sentzen) (Serpentes, Colubridae) no sudeste da Bahia, Brasil. Revista Brasileira de Zoologia 22: 573–579. https://doi.org/10.1590/S0101-81752005000300008

Balestrin RL, Di-Bernardo M (2005) Reproductive biology of *Atractus reticulatus* (Boulanger, 1885) (Serpentes, colubridae) in southern Brazil. Herpetological Journal 15: 195–199.

Balestrin RL, Di-Bernardo M, Moreno A (2007) Feeding ecology of the Neotropical worm snake *Atractus reticulatus* in southern Brazil. Herpetological Journal 17: 62–64.

Bellini GP, Arzamendia V, Giraudo AR (2013) Ecology of *Thamnodynastes hypoconia* in subtropical–temperate South America. Herpetologica 69: 67–79. https://doi.org/10.1655/Herpetologica-D-12-00027

Bizerra A, Marques OAV, Sazima I (2005) Reproduction and feeding of the colubrid snake *Tomodon dorsatus* from south-eastern Brazil. Amphibia-Reptilia 26: 33–38. https://doi.org/10.1163/1568538053693350

Braz HB, Kasperoviczus KN, Almeida-Santos SM (2014) Reproductive ecology and diet of the fossorial snake *Phalotris lativittatus* in the Brazilian Cerrado. Herpetological Journal 24: 49–57

Corn PS (1994) Straight-line drift fences and pitfall traps. In: Heyer WR, Donnely MA, McDiarmid RW, Hayek LA, Foster M (Eds) Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, DC, 109–117.

Crews D (1984) Gamete production, sex hormone secretion, and mating behavior uncoupled. Hormones and Behavior 18: 22–8. https://doi.org/10.1016/0018-506X(84)90047-3

Di-Bernardo M, Borges-Martins M, Oliveira RB, Pontes GMF (2007) Taxocenoses de serpentes de regiões temperadas do Brasil. In: Nascimento LB, Oliveira ME (Eds) Herpetologia no Brasil II. Sociedade Brasileira de Herpetologia. Belo Horizonte, 222–263.

Embrapa (2011) Estação de agrometereologia. Embrapa Centro Nacional de Pesquisa de Trigo, Passo Fundo. http//www.cnpt.embrapa.br/pesquisa/agromet [Acessed: 05/10/2016]

Ford NB, Seigel RA (1989) Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. Ecology 70: 1768–1774. https://doi.org/10.2307/1938110

Gibbons JW, Semlitsch RD (1987) Activity patterns. In: Seigel RA, Collins JT, Novak SS (Eds) Snakes: ecology and evolutionary biology. McGraw-Hill Publishing Company, New York, 184–209.

Giraudo AR, Scrocchi GJ (2000) The genus *Atractus* (Serpentes: Colubridae) in Northeastern Argentina. Herpetological Journal 10: 81–90.

Gomes CA, Marques OAV (2012) Food habits, reproductive biology, and seasonal activity of the dipsadid snake, Echinanthera undulata (Wied, 1824), from the atlantic forest in southeastern Brazil. South American Journal of Herpetology 7: 233–240. https://doi.org/10.2994/057.007.0305

Lillywhite HB (1987) Temperature, energetics and physiological ecology. In: Seigel RA, Collins JT, Novak SS (Eds) Snakes: ecology and evolutionary biology. McGraw-Hill Publishing Company, New York, 422–477.

Marques OAV, Eterovic A, Endo W (2000) Seasonal activity of snakes in the Atlantic Forest in southeastern Brazil. Amphibia-Reptilia 22: 103–111. https://doi.org/10.1163/156853801750096213

Marques OAV, Muniz-da-Silva DF, Barbo FE, Cardoso SRT, Maia DC, Almeida-Santos SM (2014) Ecology Of The Colubrid Snake *Spilotes pullatus* From The Atlantic Forest of Southeastern Brazil. Herpetologica 70: 407–416. https://doi.org/10.1655/HERPETOLOGICA-D-14-00012

Martins M, Oliveira ME (1993) The snakes of the genus *Atractus* Wagler (Reptilia: Squamata: Colubridae) from the Manaus region, central Amazonia, Brazil. Zoologische Mededelingen 67: 21–40.

Martins M, Oliveira ME (1999) Natural history of snakes in forests of the Manaus region, Central Amazônia, Brazil. Herpetological Natural History 6: 78–150.

Mathies T (2011) Reproductive cycles of tropical snakes. In: Aldridge RD, Sever DM (Eds) Reproductive Biology and Phylogeny of Snakes. Science Publishers, Enfield, 511–550. https://doi.org/10.1201/b10879-13

Panzera A, Maneyro R (2013) Reproductive biology of the snake *Liophis anomalus* (Günther, 1858, Dipsadidae, Xenodontinae). Herpetological Journal 23: 81–87.

Passos P, Fernandes R, Bérnils RS, Moura-Leite JC (2010) Taxonomic revision of the Brazilian Atlantic Forest *Atractus* spp (Reptilia: Serpentes: Dipsadidae). Zootaxa 2364: 1–63.

Pinto RR, Fernandes R (2004) Reproductive biology and diet of *Liophis poecilogyrus poecilogyrus* (Serpentes, Colubridae) from southeastern Brazil. Phyllomedusa 3: 9–14. https://doi.org/10.11606/issn.2316-9079.v3i1p9-14

Pizzatto L (2005) Body size, reproductive biology and abundance of the rare Pseudoboine snakes, genus *Clelia* and *Boiruna* (Serpentes: Colubridae) in Brazil. Phyllomedusa 4: 111–122. https://doi.org/10.11606/issn.2316-9079.v4i2p111-122

Pizzatto L, Almeida-Santos SM, Marques OAV (2007) Biologia reprodutiva das serpentes brasileiras. In: Nascimento LB, Oliveira ME (Eds) Herpetologia no Brasil II. Sociedade Brasileira de Herpetologia, Belo Horizonte, 201–221.

Pizzatto L, Cantor M, Oliveira J, Marques OAV, Capovilla V, Martins M (2008) Reproductive ecology of Dipsadine snakes, with emphasis on South American species. Herpetologica 64: 168–179. https://doi.org/10.1655/07-031.1

Prieto YA, Giraudo AR, López MS (2012) Diet and sexual dimorphism of *Liophis poecilogyrus* (Serpentes, Dipsadidae) from the wetland regions of Northeast Argentina. Journal of Herpetology 46: 402–406. https://doi.org/10.1670/10-228

Prudente ALC, Maschio GF, Yamashina CE, Santos-Costa MC (2007) Morphology, reproductive biology and diet of *Dendrophidion dendrophis* (Schlegel, 1837) (Serpentes, Colubridae) in Brazilian Amazon. South American Journal of Herpetology 2: 53–58. https://doi.org/10.2994/1808-9798(2007)2[53:MRBADO]2.0.CO;2

Quadros FLF, Pillar VD (2002) Transições floresta-campo no Rio Grande do Sul. Ciência & Ambiente 24: 109–118.

Resende FC, Nascimento LB (2015) The Female Reproductive Cycle of the Neotropical Snake *Atractus pantostictus* (Fernandes and Puorto, 1993) from South-eastern Brazil. Anatomia Histologia Embryologia 44: 225–235. https://doi.org/10.1111/ahe.12132

Rivas JA, Burghardt GM (2001) Understanding sexual size dimorphism in snakes: wearing the snakes's shoes. Animal Behaviour 62: 1–6. https://doi.org/10.1006/anbe.2001.1755

Rojas, CA, Barros, VA, Almeida-Santos, SM (2013)The reproductive cycle of the male sleep snake *Sibynomorphus mikanii* (Schlegel, 1837) from southeastern Brazil. Journal of Morphology 274: 215–228. https://doi.org/10.1002/jmor.20099

Seigel RA, Ford NB (1987) Reproductive ecology. In: Seigel RA, Collins JT, Novak SS (Eds) Snakes, Ecology and Evolutionary Biology. McMillan Publishing Company, New York, 210–252.

Shine R (1978) Sexual size dimorphism and male combat in snakes. Oecologia 33: 269–278. https://doi.org/10.1007/bf00348113

Shine R (1980) "Costs"of reproduction in reptiles. Oecologia 46: 92–100. https://doi.org/10.2307/1563569

Shine R (1982) Ecology of the Australian elapid snake *Echiopsis curta*. Journal of Herpetology 16: 388–393. https://doi.org/10.2307/1563569

Shine R (1988) The evolution of large body size in females: a critique of Darwin's "fecundity advantage"model. The American Naturalist 131: 124–131. https://doi.org/10.1086/284778

Shine R (1994) Sexual size dimorphism in snakes revisited. Copeia 1994: 326–346. https://doi.org/10.2307/1446982

Vinegar A (1974) Evolutionary implications of temperature induced anomalies of development in snake embryos. Herpetologica 30: 72–74

Vitt LJ (1987) Communities. In: Seigel RA, Collins JT, Novak SS (Eds) Snakes: Ecology and Evolutionary Biology. Macmillan Publishers, New York, 335–365.

Submitted: 1 March 2017
Received in revised form: 23 August 2017
Accepted: 4 September 2017
Editorial responsibility: Ana Lúcia Prudente

Author Contributions: NZ and FD contributed equally to this article.
Competing Interests: The authors have declared that no competing interests exist.